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RESEARCH ARTICLE

Flowering and fruiting phenology of *Solanum mauritianum* – a potential invasive alien species in the upcountry wet zone of Sri Lanka

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Abstract

First comprehensive investigation of *Solanum mauritianum* in Sri Lanka, focusing on its invasive potential, ecological traits, and management challenges in the upcountry wet zone. Field surveys (2016–2018) along the A7 road from Peradeniya to Horton Plains National Park documented rapid colonization of roadsides, agricultural lands, and disturbed habitats, driven by prolific seed production (100,000–200,000 seeds annually per mature plant), vegetative propagation, and long-distance dispersal via frugivorous birds. Phenological analyses revealed seasonal fruiting peaks (April and August) linked to temperature and humidity fluctuations, with seed dormancy broken under 12 hr light/dark cycles and gibberellic acid treatment. Self-pollination, generalist pollinator interactions, and genetic diversity (assessed via RAPD markers) further facilitated invasiveness, showing genetic clustering independent of geographic distance. Despite toxicity, farmers utilize the species for crop support, though its aggressive growth threatens native biodiversity by displacing flora. Conventional control methods, such as herbicides, proved ineffective due to rapid regrowth, while pre-fruiting uprooting and community-led management emerged as viable strategies. Community engagement enhanced data collection and invasive species awareness, underscoring participatory conservation's value. As the first study of *S. mauritianum* in Sri Lanka, this work highlights its dual role as an ecological disruptor and a resource with localized agricultural utility, emphasizing the need for adaptive management. Future research should prioritize long-term ecological impacts, biological control agents, and climate adaptation studies to refine sustainable solutions. The findings provide foundational insights for invasive species management in Sri Lanka's biodiverse ecosystems.

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Keywords
participatory community studies; invasive species; flowering; phenology

Introduction

Solanum mauritianum has an invasive potential in Sri Lanka's Central Hills by assessing its ecological spread, reproductive traits (breeding system), and genetic diversity. As the first local investigation of this globally recognized invasive species, the research sought to inform management strategies to mitigate its threat to biodiversity, given its unregulated proliferation and lack of prior impact studies in Sri Lanka. *Solanum mauritianum* is considered an invasive species in many parts of the world. In Sri Lanka, invasive alien species (IAS) have significant impacts on local biodiversity and ecosystem functioning (Global Invasive Species Database, 2019).

Impact can be insidious and most often irreversible, causing economic and ecological losses. To date, more than 32 IAS have been recorded in Sri Lanka. As one of the 34 biodiversity hotspots of the world, it is vital to have proper records on the impact of IAS on the island's rich biodiversity. *Solanum mauritianum* Scop. (Solanaceae) is among the most widespread invasive alien species worldwide. It is native to South America (northern Argentina, Uruguay, Paraguay, and southern Brazil) and was first introduced to Sri Lanka, probably by accident. The species has spread rapidly in the central and Uwa provinces in Sri Lanka during the last few years. *S. mauritianum* is an ecosystem threat in several parts of the world, including Australia, New Zealand, and Africa (Global Invasive Species Database, 2019).

S. mauritianum is a perennial small tree species up to 1.5 to 4 m tall, but sometimes 10 m and with a life span of up to thirty years (CABI, 2022). The species has become naturalized in Africa, Australasia, India, and islands in the Atlantic, Indian, and Pacific oceans, possibly via the Portuguese trade routes during the early 16th century. The plant produces gray-green, oval leaves (15 to 20 cm) covered with felt-like hairs. The leaf base has one or two ear-shaped leafy structures. Flowers are purple with a yellow center. Flowers and fruits are produced in densely branched clusters. The fruit is yellow, globular berry and 10-15 mm across (CABI, 2022). Leaves and berries of *S. mauritianum* are poisonous to humans and many other organisms, including livestock.

Solanum mauritianum contains solasodine, a steroid glycol alkaloid that can cause gastrointestinal and neurological symptoms as well as skin irritation and respiratory problems. Ingestion of the plant can be fatal to livestock, particularly cattle and horses (Cowie, 2018).

Despite its toxicity, Solanum mauritianum has been used in traditional medicine to treat a variety of ailments, including skin diseases, asthma, and hypertension (Mukherjee et al., 2011). Some studies have investigated the potential pharmacological properties of the plant, such as its antioxidant and anti-inflammatory activities (Ticona, 2022). However, further research is needed to determine the safety and efficacy of using Solanum mauritianum for medicinal purposes.

Invasive alien species (IAS) play a complex role in ecosystems and human activities, as highlighted in the manuscript. The impact of IAS is twofold as they can affect ecosystems both negatively and positively. They may decrease or increase attributes such as total biomass, or species diversity, leading to both deleterious and beneficial environmental impacts (Jeschke, 2014; Kumschick, 2012). Human Communities: These species can also influence human-related attributes, such as the number of people involved in specific activities or their income. This dual impact underscores the importance of assessing both negative and positive effects (Shackleton 2019). Focus on Deleterious Effects: The majority of research in invasion science has concentrated on the negative impacts of IAS due to the urgent need to understand their serious consequences on native communities and human activities. This focus has resulted in detailed descriptions of the mechanisms through which IAS can harm ecological and socio-economic systems (Shackleton, 2019).

Neglect of Beneficial Impacts: Despite the recognition that IAS can have beneficial effects, the literature and impact assessment frameworks predominantly evaluate deleterious impacts. This trend may lead to an oversimplified understanding of the dynamics of IAS, potentially disregarding their positive contributions. Frameworks for Assessment: The manuscript discusses the need for transparent and evidence-based frameworks that assess both positive and beneficial impacts of IAS. Such frameworks could enhance scientific understanding and inform better management practices. Value Perspectives: The arguments for considering positive impacts are categorized into value-free (quantitative changes) and value-laden (ethical and societal perceptions). This distinction is crucial for understanding how IAS are perceived and managed within different contexts (Boltovskoy, 2018; Estévez, 2015).

The significance of invasive alien species lies in their complex interactions with ecosystems and human communities, necessitating a balanced assessment of both their negative and positive impacts to inform effective management strategies. This study aimed to investigate the spread and status of *S. mauritianum*, the immediate and long-term impacts, and the ecological and economic damage to species that have not been studied in Sri Lanka. Therefore, there is an immediate need for a proper evaluation of the ecosystem and community status of the species and to understand the biological traits and population parameters that are associated with invasive behavior. Our study was focused on the growth and plant interactions, the breeding system, and the population genetic diversity of S. mauritianum in the Central Hills of Sri Lanka. The study's outcome would be beneficial for the early detection and development of strategies for effective management of the species.

Methodology

Studies on ecology and habitat

The study was performed in the upcountry wet zone representing three agro ecological zones, WU2 (Matakelle Estate, 6°55′22.9″ N, 80°42′01.2″ E), WU2 (St. Coombs Estate,

Lameliar Division, 6°55′27.6″ N, 80°41′33.9″ E) and WU3 (Desford Estate, 6°53′59.6″ N, 80°42′44.3″ E), during a two-year period from December 2016 to December 2018. Ecological surveys were performed in natural and man made forest patches in the immediate vicinity of roadsides along the A7 road.

Floral biology, phenology, and fecundity

The flowering and fruiting of *S. mauritianum* were studied in a permanent plot established at Talawakele (6°55'27.6"N 80°41'33.9"E). The work was done with community involvement. The community groups comprised students (grades 8 to 9) and teachers from three schools, members of the plantation community, and members of the "Friends of Horton Plains" environmental society. From June to November 2016, five field training sessions were conducted for the community groups, and then the community members recorded data in the data sheets provided. The floral features of the species were studied by examining flower morphology, pollen biology, and stigma receptivity. The total number of branches with flowers, branches with immature (green) fruits, and branches with mature (yellow) fruits were recorded. Weather parameters were gathered daily. Percentage floral and fruit abundance and weather parameters were analyzed using the PROC CORR procedure in SAS statistical software.

The seed germination and seedling vigor of seeds obtained from fruits collected from the same trees were studied from January to April 2016. One hundred seeds (five replicates each with 20 seeds) were germinated at 25 °C in 90 mm plastic Petri dishes containing tissue paper moistened with 500 ppm gibberellic acid (GA). Moistening with distilled water (DW) was used as the control. Seeds were germinated under the following conditions: 12 hrs./12 hr. light/dark or 24 hrs. dark conditions. Two-week-old seedlings were transplanted into plastic trays containing coir dust: compost = 1:1 medium in controlled environments or semisolid MS medium under in vitro conditions to study seedling establishment and vigor.

Genetic diversity of *S. mauritianum*

The population of *S. mauritianum* was studied based on RAPD markers, including OPAO-08, OPC-20, OPI-02, OPL-04, OPX-10, OPT-18, OPR-05, OPAB-03, OPJ-04, OPG-09, OPH-15, OPH-17, OPH-05, OPH-06, and OPB-20, and polymorphic RAPD markers were identified based on polymorphic information content (PIC). PIC was calculated by PIC = 2*fi*(1-fi). Altogether, fifteen individual plants were selected randomly from three different locations, including Site 1: Matakelle Estate (6.923037, 80.700339); Site 2: St. Coombs Estate, Lameliar division (6.924326, 80.692745) and Site 3: Desford Estate (6.899879, 80.712312). Leaves were collected from five mature (fruiting and seeding) randomly selected plants from each site for DNA extraction. DNA was extracted from 15 individuals using the CTAB protocol and screened using the selected polymorphic RAPD markers. The data were analyzed by the PROC CLUSTER procedure in SAS statistical software.

Fig. 1. (A) Dense growth of *S. mauritianum* observed on the roadside open space near Ramboda. (B) Sri Lanka map showing the study sites in the central hills. (C) Geographical distribution of the three study sites Floral morphology

Results

Ecology and habitat

During 2016, the presence and frequency of *S. mauritianum* were observed along the sides of the A7 main road from Peradeniya to Horton Plains National Park. The species was abundant on the roadsides from Ramboda up to Pattipola. Although *S. mauritianum* was only occasionally mapped beyond Pattipola during the field visits made in 2016, in 2018, we frequently observed the species along the roadsides from Pattipola to Horton Plains National Park, indicating the rapid spread of the species. We observed the species in open habitats and under shade. We also observed dense populations in nonshaded open habitats such as banks of waterways where moisture (water) was not a limiting factor. We registered these species inside tea plantations, natural forest patches, and *Pinus* plantations. In riparian habitats, the species exists in dense populations with thick canopy cover where new plants arose from underground suckers. However, along roadsides, natural forest patches, and *Pinus* plantations, individual bushes were scattered. These plants were more likely developed from seeds. These observations provide powerful evidence for rapid colonization of the species in the three studied plots.

We observed some insects on the species flowers and fruits, including bees and beetles, collecting pollen or feeding on nectar. We also mentioned several frugivorous bird species that feed on the fruits. Red-vented bulbul (*Pycnonotus cafer*) and the endemic bird species yellow-fronted barbet (*Psilopogon flavifrons*) were often observed feeding on the fruits, indicating that *S. mauritianum* provides ecological services to the local fauna. Frugivorous bird species can be long-distance seed dispersal agents of the species.

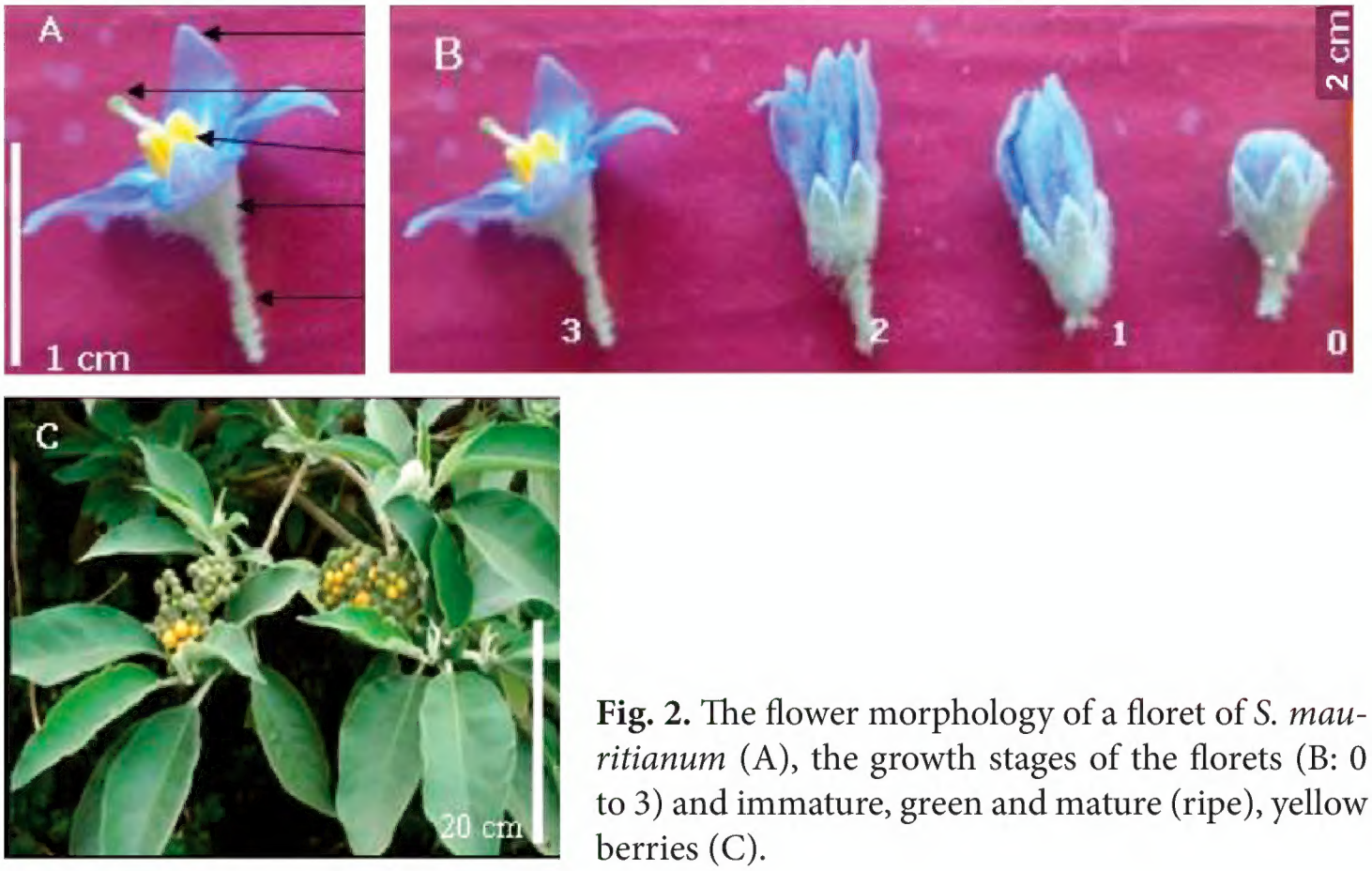

Fig. 2. The flower morphology of a floret of *S. mauritianum* (A), the growth stages of the florets (B: 0 to 3) and immature, green and mature (ripe), yellow berries (C).

Therefore, while adapting to different soil and climatic conditions, interactions with local fauna and flora show naturalization that enables the species' long-term survival.

The species produces numerous purple florets on a branched corymb. Florets were perfect and actinomorphic. Young fruits were green and globular, 10-15 mm in diameter. Once ripe, the fruits are yellow and pubescent but become glabrous with age. Berries carried many seeds (Fig. 2).

Both pollen and stigma mature in the development stage (2), signifying the absence of dichogamy (temporal barrier for selfing) in the species. The presence of perfect flowers and the absence of dichogamy indicate the potential of this species for self-pollination.

Phenology and Fecundity

We identified a seasonal pattern in flowering and fruiting phenology. We observed flowers and immature fruits throughout the year; however, there were prominent fluctuations in relative abundance (Fig. 3). Mature fruits were seasonal, and two fruiting seasons occurred in April and August. Decreased minimum temperature and daytime humidity increased the relative abundance of flowers (Pearson correlation coefficient, $r = -0.8$, $p = 0.00$ and $r = -0.6$, $p = 0.00$, respectively) and immature fruits ($r = -0.6$, $p = 0.00$ and $r = -0.7$, $p = 0.00$, respectively). However, increased minimum temperature and daytime humidity increased mature fruit abundance ($r = 0.7$, $p = 0.00$ and $r = 0.7$, $p = 0.00$, respectively).

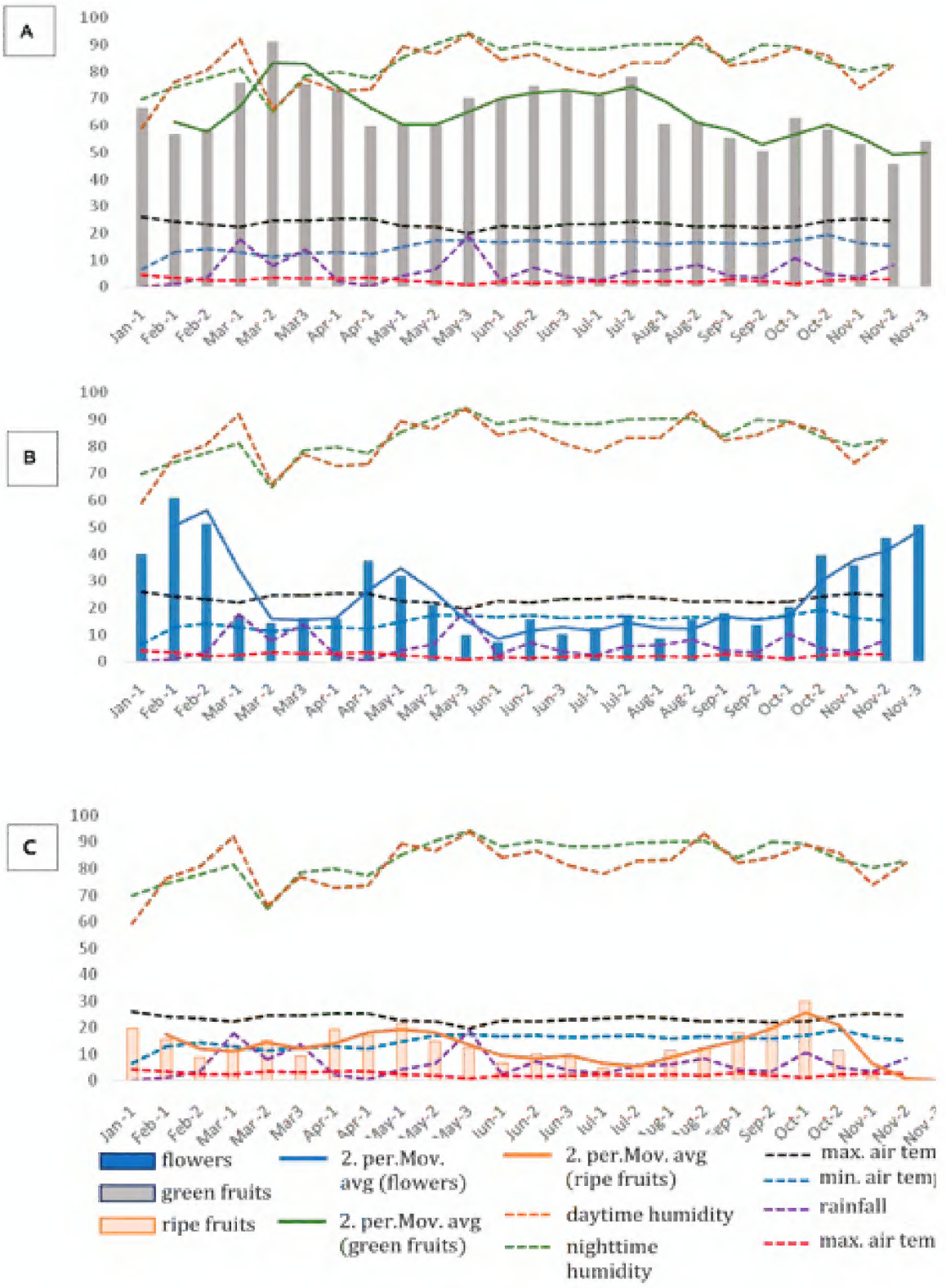

Fig. 3. Flowering and fruiting phenology of *S. mauritianum*. In each graph, the vertical axis represents: A – flowering branches (%); B – branches with green fruits (%); C – branches with mature yellow fruits (%).

Rate of seed germination and seedling vigor

Under 12 hr/12 hr light/dark conditions, the percentage germination after four weeks in 500 ppm GA was 74% higher than that in DW (23%), indicating seed dormancy in *S. mauritianum*. None of the seeds germinated after 24 hrs in the dark in DW. Seedlings did not survive in coir dust:compost medium. The seedlings survived but did not grow or produce green leaves in MS medium, showing a lack of vigor. However, during the wet season, the seedlings in the field showed growth enhancement and increased vigor.

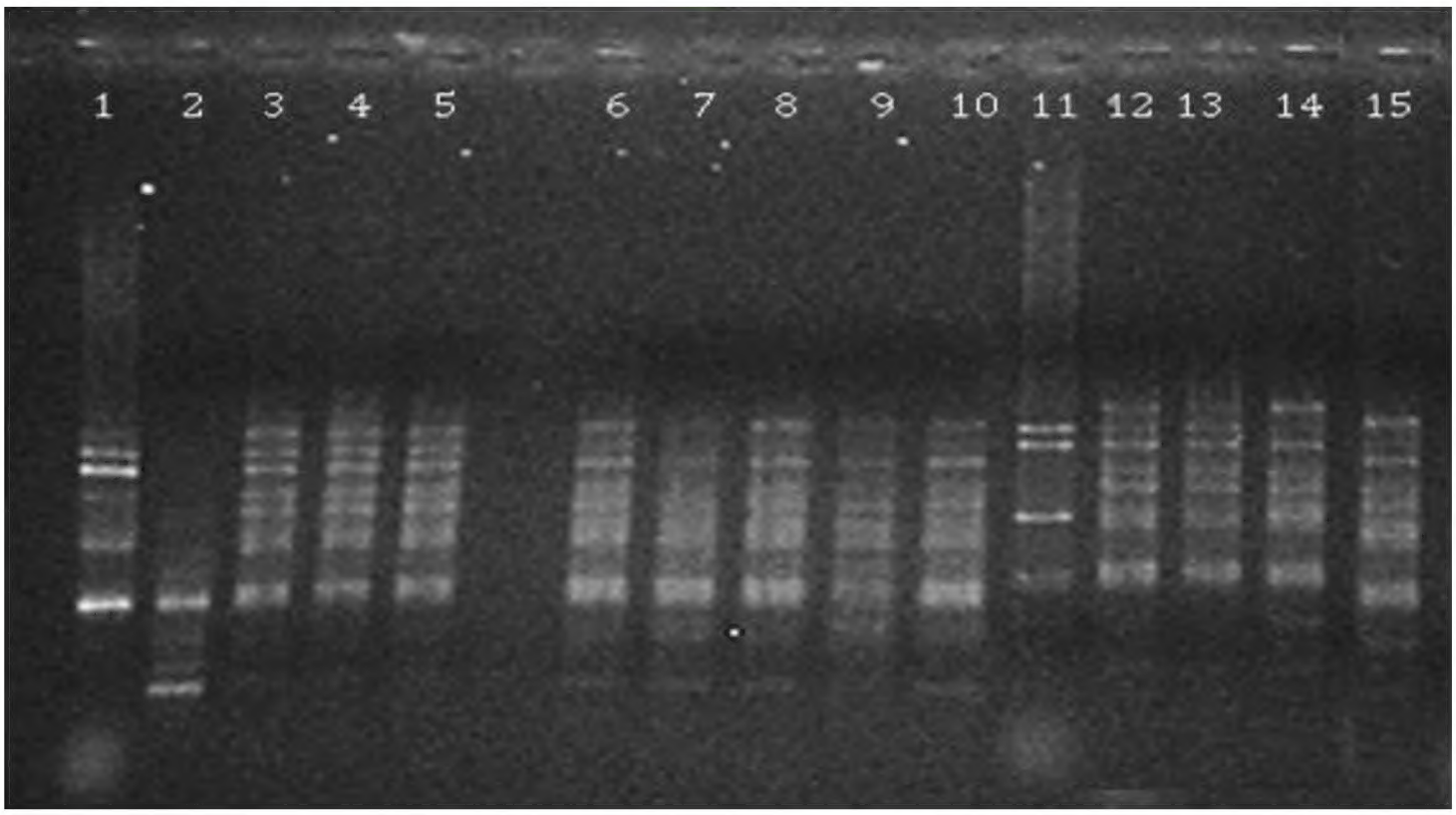

Fig. 4. RAPD using the OPH-5 primer for the fifteen individuals sampled from the three populations from Matakelle Est. site (1 to 5), St. Coombs Est. site (6 to 10) and Desport site (11 to 15).

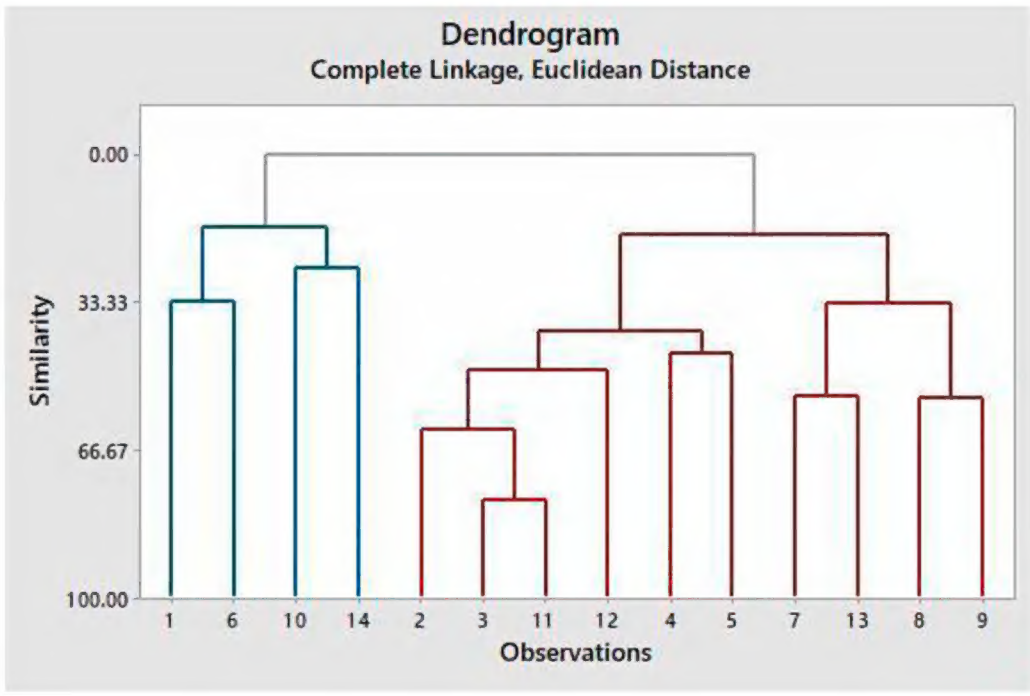

Fig. 5. Analysis of population differentiation in *S. mauritianum* based on five polymorphic RAPD primers, OPAO-08, OPC-20, OPR-05, OPJ-04, and OPH-5. Three populations from Matakelle Est. site (1 to 5), St. Coombs Est. site (6 to 10) and Desport site (11 to 15) were studied.

Population diversity and genetic structure

The plants cluster in two divergent groups. Interestingly, there was no relationship between the clustering and the location of the plants, showing that a factor other than distance between individuals causes the genetic diversity of these individuals.

Out of 15 screened markers, we identified 5 polymorphic RAPD markers: OPA-08 (PIC=0.36), OPC-20 (PIC=0.37), OPR-05 (PIC=0.46), OPJ-04 (PIC=0.31), and OPH-5 (PIC=0.36).

Discussion

Rapid growth and profuse seed production cause the rapid spread of S. *mauritianum*. We observed that seed production in *S. mauritianum* commences in plants up to 1 m in height. We observed a linear increase in seed production with increasing plant height. Mature plants taller than 3 m could produce 100,000-200,000 seeds per year. Rapid and vigorous production of seeds and vegetative propagules make *S. mauritianum* a noxious weed. It is also important to note the potentially beneficial role of S. *mauritianum* as a pioneer species that colonizes degraded sites. Therefore, the observations testified to the need for an effective management strategy to control the spread of the species while using it for economic and ecological benefits.

Despite its agricultural advantages, the species can prove to be a formidable challenge in home gardens. Its aggressive nature manifests in its rapid growth rate and deep-rooted systems, rendering it a persistent weed that can quickly overtake garden spaces. The tenacity of the species, coupled with its intricate root structure, poses a significant hurdle for gardeners attempting to control its spread and maintain a harmonious garden environment.

The study revealed the genetic diversity of *S. mauritianum* in the geographic region based on RAPD marker analysis. However, geographic distance did not determine the genetic distance. Although self-pollination of the species is reported in the literature, the authors observed frequent visits by general pollinators. However, our observation indicates the possibility of long-distance seed recruitment and cross-pollination in increasing genetic diversity in *S. mauritianum* populations. Flower heterostyles also indicate the possibility of cross-pollination and genetic diversity. Previous studies reported high levels of genetic variability within and between populations and exclusive alleles in *S. mauritianum* natural populations; however, a low correlation between genetic and geographic distance was reported. A further study on the breeding system of the species and genetic diversity of the existing populations is essential to understand the species' adaptation rates and develop effective control measures.

The study provided valuable experience working with the general community in long-term data collection and conservation projects. Furthermore, it created public awareness about invasive species and the associated environmental risks. In this study, we effectively mobilized volunteers and community support to gather regular and consistent data. Primarily, the young students worked tirelessly and with great enthusiasm and responsibility. The experience was a powerful motivation for the students to pursue science and scientific research. The knowledge and skills developed in this project could be helpful in further community-based studies.

Conclusions

This study highlights the invasive potential of *Solanum mauritianum*, demonstrating how its rapid growth, prolific seed production, and vegetative propagation enable it to dominate diverse ecosystems while outcompeting native species. The species presents significant ecological threats yet offers agricultural benefits, requiring balanced management strategies that mitigate its spread while harnessing its utility. Key findings reveal its dependence on generalist pollinators, long-distance seed dispersal, and genetic adaptability, all of which enhance its invasiveness. Additionally, the absence of natural herbivores in the study area exacerbates uncontrolled proliferation, while phenological observations suggest that timely interventions such as uprooting before fruiting can improve control measures. Community engagement proved essential in data collection and awareness campaigns, emphasizing the value of participatory conservation. Future research should focus on long-term ecological impacts, genetic and reproductive dynamics, and biological control options to better understand and manage this invasive species. Investigations into alternative control methods, economic uses, climate adaptation, and expanded community-based monitoring could further refine management approaches, ensuring more effective and sustainable solutions for controlling *S. mauritianum* while preserving native biodiversity

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